

The Role of Estuarine Habitats in Regulating Growth and Survival of Juvenile Penaeid Shrimp

Thomas J. Minello and Roger J. Zimmerman
NOAA, National Marine Fisheries Service
Southeast Fisheries Center, Galveston Laboratory
4700 Avenue U, Galveston TX 77551

Abstract

Modifications of estuarine habitats are inevitable, but information on habitat functions can be used to protect those habitats most valuable to fishery species. Density patterns of young brown shrimp in estuaries reflect the importance of macrophytic vegetation. Brown shrimp appear to be obligate carnivores, feeding on epifaunal and infaunal organisms which are frequently abundant in vegetated habitats. The structure of the vegetation also provides protection from fish predators such as the southern flounder and pinfish. A large number of environmental factors have the potential to interact with functions of vegetation, however, and the value of these habitats should be expected to vary within and among estuaries.

Distributions of juvenile white shrimp in estuaries are more variable, and information on habitat interactions is limited. This species appears to be omnivorous, having a better capacity to directly use plant foods than brown shrimp. Obvious protective adaptations to avoid predation are also less pronounced in white shrimp. Rapid growth, however, may be a predator avoidance characteristic of this species.

Introduction

Life cycles of the brown shrimp, *Penaeus aztecus*, and the white shrimp, *Penaeus setiferus*, are integrally connected with estuaries. The young of these species utilize shallow estuarine habitats, and a large part of shrimp production is supported by the productivity of these nursery areas. Unfortunately, estuarine habitats are rapidly being modified through natural phenomena and man's exploitation of coastal regions. Rising sea level, land subsidence, the alteration of fresh-water inflow, dredge and fill activities, and increased channelization and salt-water intrusion all affect estuarine habitats (Boesch *et al.*, 1983; Baumann *et al.*, 1984; Davis, 1986; Titus, 1986). Efforts to minimize the impact of habitat alterations on shrimp stocks require an understanding of the relative value of habitats for shrimp and the

mechanisms through which habitats influence growth and survival. Estuaries in the northern Gulf of Mexico support the largest populations of brown shrimp and white shrimp in the U.S. (Klima, 1981), and coastal habitats in this region are especially threatened (Bauman *et al.*, 1984; Titus, 1987). In response, recent investigations in ecology at the Galveston Laboratory of the National Marine Fisheries Service have been directed towards understanding the functional importance of estuarine habitats for penaeid shrimp. This paper is a review and synthesis of research on habitats, growth, and mortality of brown shrimp and white shrimp in estuarine nurseries.

Shrimp Distributions in Estuaries

Density patterns of juvenile shrimp in estuaries appear to be useful as indicators of habitat value. In Mobile Bay, Loesch (1965) reported that small brown shrimp were associated with the submerged vegetation *Ruppia* and *Vallisneria* and that white shrimp were found on nonvegetated bottom with large amounts of organic detritus. Williams (1955) had previously noted an association between white shrimp distributions and detritus-rich sediments in North Carolina estuaries. Stokes (1974) reported that white shrimp were more frequently found on nonvegetated bottom near Laguna Madre, Texas, and that brown shrimp were on both nonvegetated bottom and in seagrass beds. Extensive comparisons of estuarine habitats, however, have been hampered by inefficient sampling methods (Zimmerman *et al.*, 1986). The development of a drop-sampling technique by Zimmerman *et al.* (1984) has improved our ability to quantitatively sample shallow vegetated habitats, including intertidal marsh. Using this technique we have established that during most of the year, young brown shrimp in Galveston Bay, Texas strongly select for *Spartina alterniflora* habitat over nonvegetated bottom (Figure 1). Similar samples taken in the estuaries of both Texas and Louisiana, have shown that brown shrimp frequently select for a wide variety of vegetated estuarine habitats including intertidal marsh vegetation (*Spartina alterniflora*, *S. patens*, *Juncus roemerianus*, and *Scirpus robustus*) and submerged vegetation (*Halodule wrightii* and *Ruppia maritima*). There is now substantial evidence that brown shrimp frequently select vegetated habitats over nonvegetated bottom in estuaries of the northern Gulf of Mexico. Selection

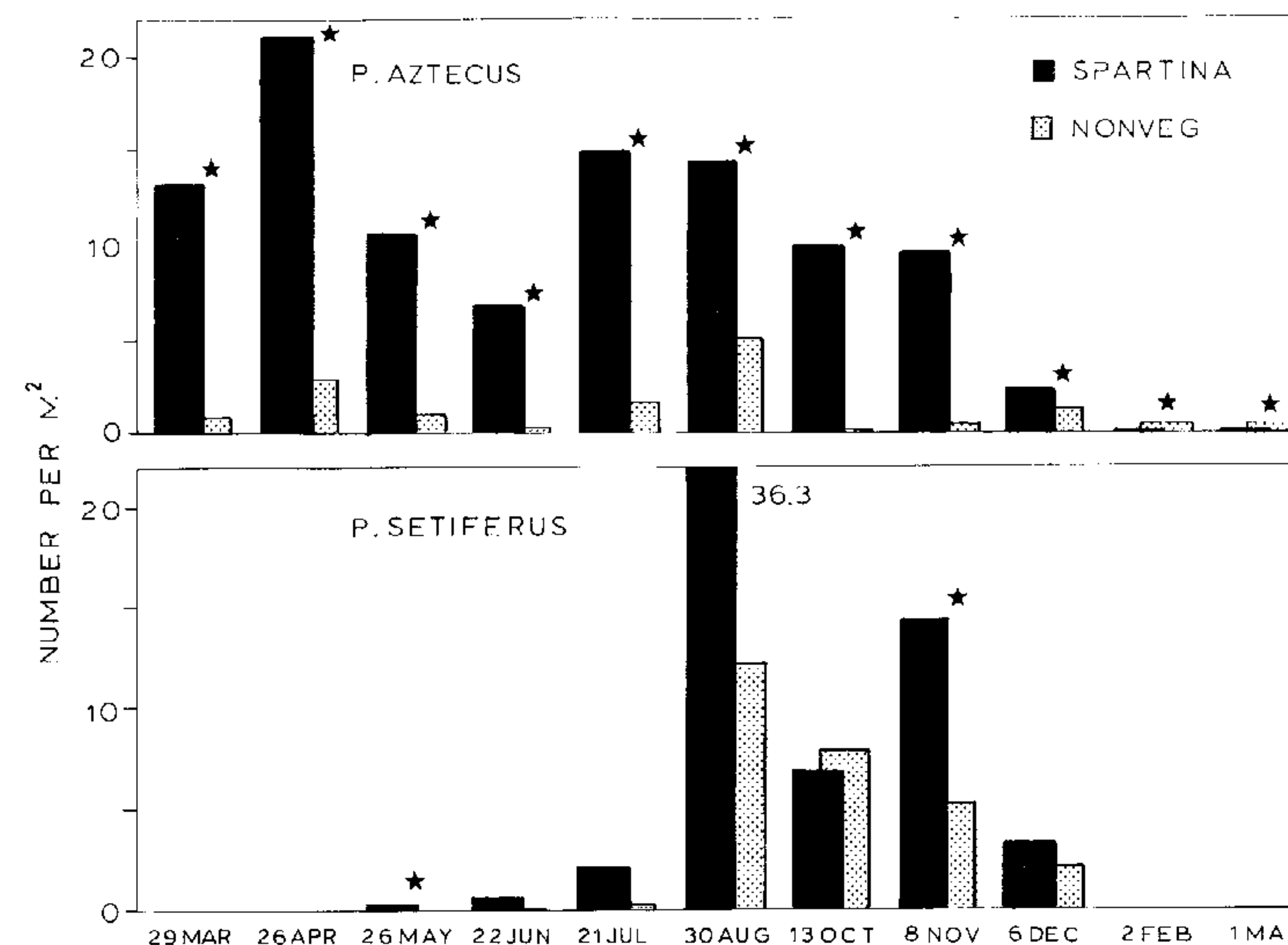


Figure 1. Mean densities of *Penaeus aztecus* and *P. setiferus* collected within intertidal *Spartina alterniflora* habitat and on adjacent nonvegetated bottom. Asterisks indicate significant selection for a habitat based on a comparison of shrimp densities from 12 pairs of drop samples collected on each date (paired t-test, 5% significance level). Data are from Zimmerman and Minello (1984).

patterns for white shrimp are less clear, and in Galveston Bay (Zimmerman and Minello, 1984) white shrimp did not consistently select for *Spartina* or nonvegetated bottom (Figure 1).

Density patterns, however, may not always reflect the value of estuarine habitats. Animals can aggregate in habitats with little food or protective value simply due to current patterns or due to evolutionary selective forces which are no longer in synchrony with habitat value. In contrast, relatively unpopulated habitats may indirectly provide food to organisms or serve as migratory pathways. Determining the importance of various habitats for penaeid shrimp requires information on how habitats function to regulate growth and survival.

Natural Diets and Habitat-related Growth

An understanding of the natural feeding habits and diets of penaeid shrimp in estuaries has been elusive. In part, this can be attributed to variability in diet among species and to ontogenetic changes within species (Stoner and Zimmerman, 1988). Large amounts of detrital material are available in estuaries (de la Cruz, 1965), and detritus has frequently been reported in the gut contents of shrimp (Williams, 1955; Darnell, 1958; Odum and Heald, 1972; George, 1960; Jones, 1973; Chong and Sasekumar, 1981). For this reason, plant detritus and associated bacteria have been believed to be directly important to shrimp nutrition (Moriarty, 1976; 1977). Gleason and Zimmerman (1984), however, have shown that for postlarval brown shrimp, *Spartina* detritus alone does not provide enough nutrition for growth or body maintenance. They also showed that plant material, including epiphytic algae scraped from *Spartina alterniflora* stems, could provide sufficient nutrition for maintenance of small brown shrimp but not enough to sustain normal growth. Considering the apparent requirement for animal protein in shrimp diets (Condrey *et al.*, 1972; Venkataramiah *et al.*, 1975; Zein-Eldin and Corliss, 1976), benthic infauna and epifauna are probably important foods. This conclusion is supported by evidence that meiofauna and small macrofauna (haracticoid copepods, amphipods and polychaetes) are nearly always present in shrimp guts (Dall, 1968; Moriarty, 1977; Marte, 1980; Hunter and Feller, 1987; Stoner and Zimmerman, 1988), and depletion of these organisms occurs in experimental enclosures with shrimp (Gleason and Zimmerman, 1984; Leber, 1985; Gleason and Wellington, 1988; and Zimmerman *et al.*, in review). These small fauna used as food by shrimp are generally considered to be components of food webs based on aged detritus, algal epiphytes, and macroalgae. Conflicting evidence still exists, however, as to the relative contribution of benthic versus planktonic sources of carbon in shrimp food webs (Fry, 1981; Hughes and Sherr, 1983; Gleason, 1986; Gleason and Wellington, 1988; Stoner and Zimmerman, 1988).

The relationships between food abundance, habitat value, and shrimp growth have been examined in field and laboratory experiments by Zimmerman *et al.* (in

review). Brown shrimp enclosed in cages with access to *Spartina alterniflora* marsh surface grew faster than in cages restricting them to nonvegetated bottom (Table 1). By contrast, growth rates of white shrimp in the two habitats were not significantly different. Elevated abundances of small benthic macrofauna have been associated with *Spartina alterniflora* marshes (Rader, 1984), and the availability of these animals was apparently responsible for the increased growth of brown shrimp in the cages with *Spartina*. Cores taken during the experiment showed that populations of peracarid crustaceans and polychaetes were largest within *Spartina* cages, and their populations were depleted in the cages with high densities of brown shrimp (Zimmerman *et al.*, in review). Laboratory experiments conducted during the study confirmed that both brown shrimp and white shrimp fed on infauna and epifauna, but feeding by brown shrimp was more efficient (Table 2).

Such studies demonstrate that there is a nutritional component to habitat selection patterns of juvenile brown shrimp, and that the value of vegetation differs among shrimp species. The data from Zimmerman *et al.* (in review) indicate that brown shrimp are carnivorous, and that amphipods, tanaids, and polychaetes present in *Spartina alterniflora* habitats are a primary source of nutrition for this species. Seasonal differences in the distributions of food organisms may account for the apparent reversal in habitat selection by brown shrimp during the early spring (Figure 1).

White shrimp are less efficient feeders on benthic fauna (Table 2), and appear to incorporate more plant material into their diet. In ponds with mainly phytoplankton present as food, high growth rates reported for white shrimp (Johnson and Fielding, 1956; Wheeler, 1968) suggest that this species has the capacity for direct utilization of plant materials. Laboratory experiments by McTigue and Zimmerman (unpublished) show that the growth response of white shrimp is significantly greater than that of brown shrimp when diatoms are added to animal protein diets. The ability to exploit a wide variety of plant and animal foods might explain the apparent lack of a strong habitat selection pattern by white shrimp. More information on preferred foods and the distribution of these foods is needed to understand interactions between white shrimp and estuarine habitats.

Mortality in Estuarine Nurseries

The role of estuarine habitats in regulating mortality of juvenile shrimp depends upon the magnitude and variability of mortality in estuaries and upon the major causes of mortality. Minello *et al.* (1989) measured brown shrimp mortality using a length-frequency analysis of cohorts from drop sample data in a Galveston Bay salt marsh, and actual mortalities for 2-week periods during the spring of 1982 ranged from 33% to 61% (Figure 2). Other estimates (adjusted to 2-week rates) of 52% for subadult *Penaeus aztecus* (McCoy, 1972) and 65% for juvenile *Penaeus vannamei* (Edwards, 1977) would also indicate that mortality in estuaries can have a large impact on adult populations.

Adverse physical conditions can cause mortality of penaeid shrimp in estuaries, but these catastrophic events appear to be relatively rare. Gunter (1941) and Gunter and Hildebrand (1951) documented cold-related kills of shrimp in Texas estuaries, and similar phenomena have been observed along the southeastern coast of the U.S. (Dahlberg and Smith, 1970). However, cold fronts mainly occur during winter and early spring months, and during most of the time when young shrimp occupy estuarine nurseries, temperatures do not appear to reach levels known to be lethal (Zein-Eldin and Aldrich, 1965; Zein-Eldin and Griffith, 1969; Zein-Eldin and Renaud,

Table 1. Habitat-related summer growth rates of juvenile *Penaeus aztecus* and *P. setiferus* caged together in *Spartina alterniflora* and on non-vegetated bottom. The largest initial size possible (32mm, TL) was used in calculations and growth rates are conservative. (from Zimmerman *et al.*, in review).

	growth in mm/day(1SE)	
	<i>Spartina</i>	Non-vegetated
<i>P. aztecus</i> (high density)	0.98 (0.02)	0.77 (0.03)
<i>P. aztecus</i> (low density)	1.41 (0.05)	1.03 (0.13)
<i>P. setiferus</i> (low density)	1.04 (0.03)	1.05 (0.05)

1986). Persistent hypoxic conditions (dissolved oxygen less than 2 mg/ml), which occur during summer months in estuaries and shallow coastal regions (Gunter, 1942; May, 1973; Turner *et al.*, 1987), can also potentially cause shrimp mortality.

Juvenile brown shrimp, however, can survive in waters with dissolved oxygen less than 1 mg/ml (Kramer, 1975), and Renaud (1986) has shown that, at least in the laboratory, both brown shrimp and white shrimp can detect and avoid oxygen depleted water. Juvenile penaeid shrimp have been collected over a wide range of temperatures, salinities, and dissolved oxygen levels, and laboratory studies indicate that these factors are unlikely to be major direct causes of shrimp mortality (see Zein-Eldin and Renaud, 1986 for review). Food supplies in estuaries seem adequate to prevent starvation (Gleason and Zimmerman, 1984; Zimmerman *et al.*, in review, and parasitism and disease do not appear to be a major direct cause of mortality in natural populations (Overstreet, 1973; Couch, 1978). Predation by fishes, however, is common, and many analyses of stomach contents have identified fish predators on shrimp (see Minello and Zimmerman, 1983 for review). The importance of predation as a cause of mortality is supported by results from field caging experiments in which 2-week mortalities of brown shrimp during the spring were less than 3% when predators were excluded (Minello *et al.*, 1989).

Table 2. Depletion of peracarid crustaceans (Amphipoda and Tanaidacea) and annelid worms (Polychaeta and Oligochaeta) from shrimp feeding in 78.5 cm² benthic cores taken from a Galveston Bay salt marsh. Individual 28-mm shrimp were placed in 12 cores per treatment, and the values shown are mean numbers of prey organisms remaining after 5 days. In ANOVA's comparing the three treatments, all means were significantly different (5% level) except those indicated by a connecting line. (from Zimmerman *et al.*, in review).

Prey	Treatments		
	Control	<i>P. setiferus</i>	<i>P. aztecus</i>
Peracarida	13.5	7.1	1.6
Annelida	37.0	10.2	3.9
Total	50.5	17.3	5.5

The dominant predator on penaeid shrimp during the spring in a Galveston Bay marsh was the southern flounder, *Paralichthys lethostigma* (Table 3). Pinfish, *Lagodon rhomboides*, spot, *Leiostomus xanthurus*, and gulf killifish, *Fundulus grandis*, also fed upon penaeids. Young spotted seatrout, *Cynoscion nebulosus*, and red drum, *Sciaenops ocellatus*, were important predators on penaeids during the late summer and fall (Table 3).

Habitat characteristics that modify predation rates of fishes can regulate shrimp mortality, and predation rates on brown shrimp are affected by vegetation (Minello and Zimmerman, 1983; 1985; Minello *et al.*, 1989), substrate type, and water clarity (Minello and Zimmerman, 1984, Minello *et al.*, 1987). In addition, other environmental conditions such as temperature, salinity, and food availability, that may only have a limited direct effect on shrimp mortality, can regulate mortality by mediating the impact of predation.

Estuarine vegetation has been shown to reduce predation by fishes on a variety of prey (Van Dolah, 1978; Coen *et al.*, 1981; Heck and Thoman, 1981; Lascara, 1981; Wilson *et al.*, 1987). Because the dominant estuarine vegetation in the northwestern Gulf of Mexico is intertidal salt marsh, water levels and hydroperiod become important in regulating predation and mortality. Laboratory predation rates on brown shrimp increased with shrimp density and decreased in the presence of *Spartina alterniflora* (Minello *et al.*, 1989). Water levels in the marsh control access to intertidal vegetation, and to some extent control prey densities. On flood tides, brown shrimp are concentrated within protective vegetated habitats, but low tide conditions result in high densities of both shrimp and fish predators on nonvegetated bottom. Extended periods of abnormally low water probably increase brown shrimp mortality, and standing high water which normally occurs during the spring in the northern Gulf of Mexico (Hicks *et al.*, 1983; Bauman, 1987) probably decreases mortality. Thus, seasonal and geographic differences in tidal dynamics and hydroperiod may play an important role in shrimp survival.

Physical conditions and the type and quantity of food available can regulate shrimp growth (Zein-Eldin and Aldrich, 1965; Zein-Eldin and Griffith, 1969; Gleason and Zimmerman, 1984; Zimmerman *et al.*, in review), and growth rates may interact with predation. Size-selection experiments with spotted seatrout

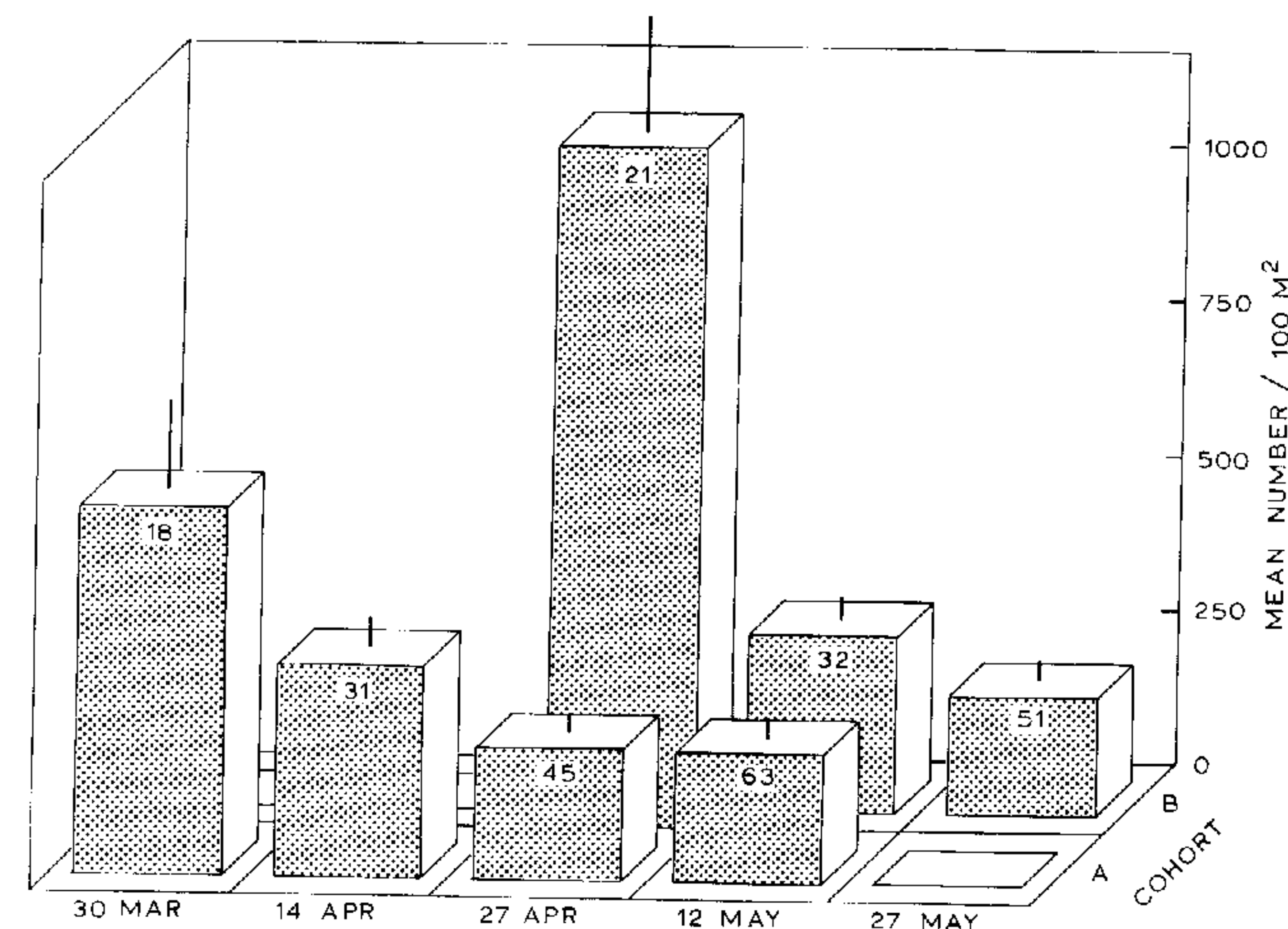


Figure 2. Mean densities of *Penaeus aztecus* in two cohorts identified through a length-frequency analysis. Decreases in density over time represent mortality. Samples were collected in a Galveston Bay salt marsh during the spring of 1982. The mean size (mm, total length) of shrimp in each cohort is shown on the histograms. Error bars are 1 SE of the mean. (from Minello *et al.*, 1989.)

(Minello and Zimmerman, 1983; 1984) and with southern flounder (Minello *et al.*, 1989) indicate that these predators select small shrimp, and the optimal prey size is less than 1/3 to 1/2 the total length of the predator. Rapid growth by shrimp should reduce the time spent at this optimal prey size, and a refuge from predation by juvenile estuarine fishes may be found with increased size. This hypothesis is supported by an apparent reduction in mortality of the larger size classes of young brown shrimp (Figure 2). Environmental conditions and food abundances which affect growth rates may regulate mortality through this mechanism.

The environment can also interact with mortality of shrimp through its effect on protective behaviors. Burrowing in the substratum has been shown to protect brown

shrimp from predation by southern flounder and pinfish (Minello *et al.*, 1987).

Light intensity at the substrate surface has a large effect on burrowing (Wickham and Minkler, 1975; Lakshmi *et al.*, 1976; Minello *et al.*, 1987), and other environmental conditions including temperature (Fuss and Ogren, 1966; Aldrich *et al.*, 1968), salinity (Venkataramiah *et al.*, 1974; Lakshmi *et al.*, 1976), dissolved oxygen (Egusa and Yamamoto, 1961), and the type of substratum (Rulifson, 1981; Aziz and Greenwood, 1982) can affect burrowing rates. All of these factors have the potential to modify mortality rates of shrimp.

Predator avoidance behaviors appear to be better developed in brown shrimp than in white shrimp. Selection for protective vegetation (Minello and Zimmerman, 1985) and the strong tendency to burrow into the substratum (Wickham and Minkler, 1975) are traits of brown shrimp. White shrimp also burrow, but the burrows are shallow and the frequency is reduced (Williams, 1958). Increased vulnerability to predators from reduced burrowing, may be offset by increased foraging time for white shrimp which should result in increased growth. White shrimp post-larvae generally arrive in estuaries during the late spring and summer (Baxter and Renfro, 1967), when increased water temperatures should also stimulate growth. Reported growth rates for white shrimp are generally higher than those of brown shrimp (see Knudsen *et al.*, 1977; Christmas and Etzold, 1977 for reviews), and this may reduce the time white shrimp are available to predators.

Conclusions

Modifications of estuarine habitats are inevitable, but information on habitat functions can be used to protect those habitats most valuable to fishery species. The importance of estuarine vegetation is strongly indicated for brown shrimp. Brown shrimp appear to be obligate carnivores, feeding on epifaunal and infaunal organisms which are frequently abundant in vegetated habitats. The structure of the vegetation also provides protection from fish predators such as the southern flounder and pinfish. A large number of environmental factors have the potential to interact with functions of vegetation, and the value of these habitats should be expected to vary within and among estuaries.

Information on habitat interactions for white shrimp is limited. This species

Table 3. Dominant fish predators on penaeid shrimp. Stomach contents of fish were analyzed to determine the frequency of feeding on *Penaeus*. (taken from Minello *et al.*, 1989).

Species	Number of fish examined	Size range (mm,TL)	March - May 1982		
			Number with food	Percent ^a with <i>Penaeus</i>	Percent ^b of all(11) <i>Penaeus</i> eaten
Southern flounder	21	34-143	19	33.3	72.7
Gulf killifish	15	24-85	13	6.7	9.1
Pinfish	254	12-64	252	0.4	9.1
Spot	180	16-75	112	0.6	9.1

Species	Number of fish examined	Size range (mm,TL)	March 1982 - September 1984		
			Number with food	Percent with <i>Penaeus</i>	Percent of all (56) <i>Penaeus</i> eaten
Southern flounder	38	34-184	31	31.6	28.6
Spotted seatrout	116	11-135	95	15.5	46.4
Red drum	59	8-131	34	3.4	14.3
Gulf killifish	102	21-88	77	2.0	3.6
Pinfish	483	15-84	459	0.6	5.4
Spot	267	18-110	183	0.4	1.8

^a Percentage of fish examined having eaten at least one *Penaeus*.

^b Percentage of the total number of *Penaeus* found in all fish examined (shown in parentheses).

appears to be omnivorous, having a better capacity to directly use plant foods than brown shrimp. Obvious protective adaptations to avoid predation are also less pronounced in white shrimp. Rapid growth, however, may be a predator avoidance

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